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Amphispongieae, A New Tribe of Paleozoic Dasycladaceous Algae

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ABSTRACT

Amphispongia oblonga Salter, 1861 is a Silurian problematic organism from Scotland originally described as a sponge. It forms the base of the lyssakid family Amphispongiidae Rauff, 1894. It has been suggested that the fossil may be an alga (Finks, 1967) which is now accepted, and *Amphispongia* is here redescribed as a dasycladacean alga. A new tribe Amphispongieae comprising *Amphispongia* Salter, 1861 and *Anomaloides* Ulrich, 1878 is erected.

HISTORICAL BACKGROUND

Salter (1861) described and illustrated *Amphispongia oblonga* as a new genus and species of calcareous sponge from the Silurian Ludlovian rocks of the vicinity of Edinburgh, Scotland. He compared his genus to the recent sponge *Grantia*, and considered that *Amphispongia* together with the genera *Ischadites*, *Favospongia*, *Tetragonis*, and *Receptaculites* belong to one family. Later, Salter (1873) further emphasized that these genera together with *Sphaerospongia* are allied to the living *Grantia*.

Various nineteenth century authors listed *Amphispongia* either among the Amorphozoa, under Protozoa, or in various taxa of sponges (Bigsby, 1868; Murchison, 1872; Roemer, 1876; Zittel, 1877–1880; Etheridge, 1888; and Head, 1895).

Hinde (1883, 1884, 1887, 1888) studied *Amphispongia* in great detail. He considered that the upper part of the organism clearly shows a relationship to lyssacine hexactinellids, but the lower parts are different from any known fossil siliceous sponges. Therefore, he was not able to place *Amphispongia* in any definite position

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among hexactinellids. He interpreted the lateral projections as spicules, and hence concluded that the organism is an abnormal hexactinellid. Nicholson and Lydekker (1889), however, believed that in spite of its aberrant character, *Amphispongia* should be regarded as belonging to the Hexactinellidae. Rauff (1894) also had no doubt that in spite of its peculiarities and aberrant traits *Amphispongia* is a real lyssacine and erected a new family Amphispongiidae for this genus. Ulrich (1895) placed his new genus *Anomaloides* among receptaculitids and noticed the morphologic similarities between *Amphispongia* and *Anomaloides* and suggested that these two are a new, as yet unnamed family or order, separate from all other receptaculitids.

Recently Lamont (1947, 1961) and Mitchell (1962) listed *Amphispongia* as a common fossil in the Pentland Hills of Edinburgh, Scotland. Laubenfels (1955) in the *Treatise on Invertebrate Paleontology,* also formally assigned *Amphispongia* to the Amphispongiidae in the order Lyssakida of the class Hyalospongea. Likewise, in the *Osnovy Paleontologii,* Rezvoi et al. (1962) expressed no doubt of the sponge nature of *Amphispongia* and consider Amphispongiidae a family among Lyssacina. Finks (1967) believed that *Amphispongia* resembles the receptaculitids in structure. He assigned receptaculitids tentatively to the Porifera but suggested that they may possibly be algae. He further indicated that *Pirania* Walcott may be a related form. Nitecki (1970) redescribed *Anomaloides* as a dasycladacean alga, and reviewed Ulrich's (1895) suggestion of the relationship of *Amphispongia* to *Anomaloides,* thus implying the algal nature of *Amphispongia.*

ALGAL NATURE OF THE *AMPHISPONGIA*

It is only recently that the algal nature of the *Amphispongia* has been suggested. It is also only recently that the receptaculitids have been identified as algae. It is deemed necessary at this time to review certain aspects of the paleontologic reasoning responsible for this late recognition of the nature of the organism.

Five Kingdoms: There has been, in the past, a discussion of proper assignment of "lower" organisms and a controversy over how many kingdoms of organisms should be recognized. The traditional concept of two kingdoms is now difficult to defend and a proposal for five kingdoms has been made (Whittaker, 1969). While it is very troublesome to accept three kingdoms (Nitecki,

1957), the five kingdoms system seems to be a logical and a workable concept. Briefly Whittaker's scheme consists of the following Kingdoms: Monera (procaryotic organisms), Protista (unicellular forms), Plantae (photosynthesizing plants), Fungi (absorptive plants), and Animalia ("conventional" animals). We are here concerned with those fossils that could be considered to belong to Plantae in the new five kingdoms system.

PLANTS VS. ANIMALS: The many differences between plants and animals are best manifested among so-called higher plants and animals. In general, a plant is an organism that manufactures its own substance from simple inorganic compounds with the aid of light energy. It is the nature of this "food," the gaseous carbon dioxide from the atmosphere and the liquid water percolating down the soil, that is responsible for the basic architectural pattern of plants. Plant leaves have large external surface areas and plant roots consist of elongated branches. This nature of food requires a continuous growth extension of the surface area and of the root systems. Associated with this growth pattern is the rigid cell wall support. Animals by contrast are characterized by the lack of ability to synthesize their food requirements and are, therefore, required to "eat" large molecules. Animals, like saprophytic plants, are unable to manufacture carbohydrates and amino-acids from simpler molecules, and have evolved the adaptation of ingesting organisms that already contain these molecules. As a result, animals generally have locomotion and their architecture consists of a compact body surrounding the large internal surface of a central digestive cavity. Thus, by comparison with plants, the animals' external "surface area" is reduced, and no need for continuous growth exists. Therefore, animals are of more uniform size and possess a central axis and have lateral (or radial) symmetry.

In fossil condition the preserved parts are only structural and when ovoid or claviform organisms with a central axis or vacuity are found they are considered to be animals. *Amphispongia*, architecturally, together with many other Paleozoic forms, possess this compact body form, a relatively small size, the central axis, and a limited growth. In addition, the lateral branches and the stellate structures have been misinterpreted as spicules, and, therefore, *Amphispongia* has been considered a sponge.

ALGAE: In the nineteenth century (and sometimes even today) algae were considered alive in a lesser degree than animals and were generally thought of as sea weeds, pond scum, and kelp. Algae are,

however, a highly diversified group and within the recent five kingdoms division are assigned to three: Monera, Protista, and Plantae! Yet, seldom is a compact small organism with a central axis considered algal by persons other than neophycologists. Forms heavily encrusted with calcium carbonate and with compact thalli are very common algae, particularly among siphonous algae, where a distinct differentiation into a well-defined thallus is not infrequent.

Interpretation of the nature of the fossil is particularly complicated when instead of actual skeletons only molds or casts are preserved.

Algal Character of *AMPHISPONGIA*: *Amphispongia* possesses a specialized thallus organized into a main axis and laterals borne in the upper part distinctly in whorls. The growth of the thallus and the growth of the branches is limited. The heavy calcification is of dasycladaceous habit. The rhizoidal base is assumed to have been present, but since it is not preserved it is believed to have been uncalcified.

Relationship: *Amphispongia* is indeed closely related to *Anomaloides* Ulrich, which has been recently redefined and redescribed as a dasycladacean alga (Nitecki, 1970). Nitecki reconstructed the anatomy of *Anomaloides* and showed that the plant is claviform and its attachment may have been rhizoidal. Its main axis is non-calcified and laterals are packed in whorls. The upper younger laterals and the rhizoidal portions are not preserved and are hence also assumed to have been uncalcified. *Amphispongia,* on the other hand, possesses the younger, immature laterals preserved. It is possible that *Anomaloides* possessed similar, although uncalcified, branches.

The differences between these two genera are in the arrangement of lower laterals (regular in *Anomaloides* but randomly arranged in *Amphispongia*) and in the character of the terminal structure of laterals. In *Anomaloides,* these are small and thin and are considered second-degree branches. In *Amphispongia,* they are stellate structures, cross-like, and similar to corresponding structures in *Cyclocrinites darwini* and *Ischadites iowensis.*

Finks (1967) suggested the relation of *Amphispongia* to the Middle Cambrian *Pirania muricata* Walcott. The illustration and description of *Pirania* (Walcott, 1920) are indeed highly suggestive of close affinity between these two genera, and Finks' (1967) suggestion appears valid. If this probable relationship proves correct

upon restudy of *Pirania*, then the three genera will constitute a taxon extending stratigraphically from the Middle Cambrian to the Silurian.

SYSTEMATIC DESCRIPTION

Chlorophyceae Kützing, 1845
Dasycladales Pascher, 1931
Receptaculitaceae Eichwald, 1860
Amphispongieae trib. nov.

Amphispongidae. Rauff, 1894, Palaeosp., p. 275.

Amphispongiidae. Laubenfels, 1955, Treat. Invert. Paleo., part E., p. 77; Rezvoi, Zhuravleva and Koltun, 1962, Osnovy paleontol., pp. 27, 41.

Cyclocriniteae. Nitecki, 1970, Fieldiana: Geol., **21** (in part), pp. 57–58.

Definition.—Small, solitary, dasycladaceous marine alga; thallus ovate, claviform or irregular; main axis rarely branched; laterals mostly in whorls; basal branches claviform; apical filamentous; 2, 3, or 4 hairs or stellate structures apically on branches; calcification of laterals and lateral hairs only; Upper Ordovician (Cincinnatian) to Silurian (Ludlow); North America and Scotland; two genera: *Amphispongia* Salter, 1861 and *Anomaloides* Ulrich, 1878.

Discussion.—Nitecki (1970) demonstrated the algal nature of *Anomaloides* which he considered a cyclocrinitid. Its algal nature appears well documented; however, its assignment among cyclocrinitids is now questioned. The suggestion of the relationship of *Anomaloides* and *Amphispongia* is now confirmed and the two genera are united in one tribe.

Whether *Pirania* Walcott, 1920 belongs in this group can only be answered after *Pirania* is restudied.

Anomaloides Ulrich, 1878

Definition.—Thallus elongated; laterals branched into second degree; first degree straight, in densely packed whorls, trifurcating into second order; facets weak, formed by secondaries; Ordovician, Maysville, Kentucky; one species.

Amphispongia Salter, 1861

Amphispongia Salter, 1861, Mem. Geol. Surv. Great Brit. Scotland, pp. 135, 136; Salter, 1873, Cat. Camb. Silur. fossils, p. 99; Zittel, 1877, Studien,

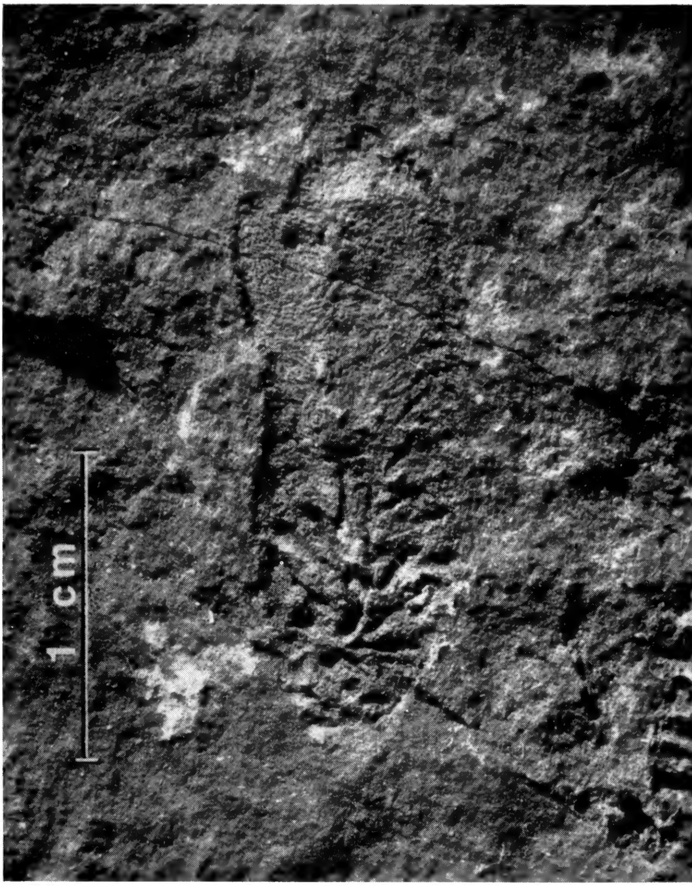

FIG. 1. *Amphispongia oblonga* Salter, 1861. Royal Scottish Museum—Geology no. 1897.32.776. A relatively well preserved, complete specimen.

München, p. 45; Zittel, 1877, N. Jahr. Min., p. 354; Zittel, 1877, Stud. Ann. Mag. Nat. Hist., p. 502; F. Roemer, 1880, Lethaea Pal., p. 317; Zittel, 1880, Handb. Paleontol., p. 173; Hinde, 1883, Cat. foss. sponges, pp. 10, 16, 154; Hinde, 1884, Quart. Jour. Geol. Soc. London, **40**, pp. 810, 818; Hinde, 1887, Mono. Brit. fossil sponges, part 1, p. 22; Hinde, 1888, Mono. Brit. fossil sponges, part 2, pp. 96, 97, 120–131; Nicholson and Lydekker, 1889, Man. Palaeontol., **1**, pp. 176–177; Rauff, 1894, Palaeosp., pp. 275–276; Head, 1895, Palaeo. sponges, p. 6; Ulrich, 1895, Geol. Minn., **3**, pt. 1, pp. 73, 74; Laubenfels, 1955, Treat. Inv. Paleo., part E., p. 77; Finks, 1967, Fossil rec., p. 340; Nitecki, 1970, Fieldiana: Geol., **21**, pp. 65–66.

Definition.—Thallus ovate or claviform; claviform basal laterals at random; upper filamentous laterals in whorls; stellate structures

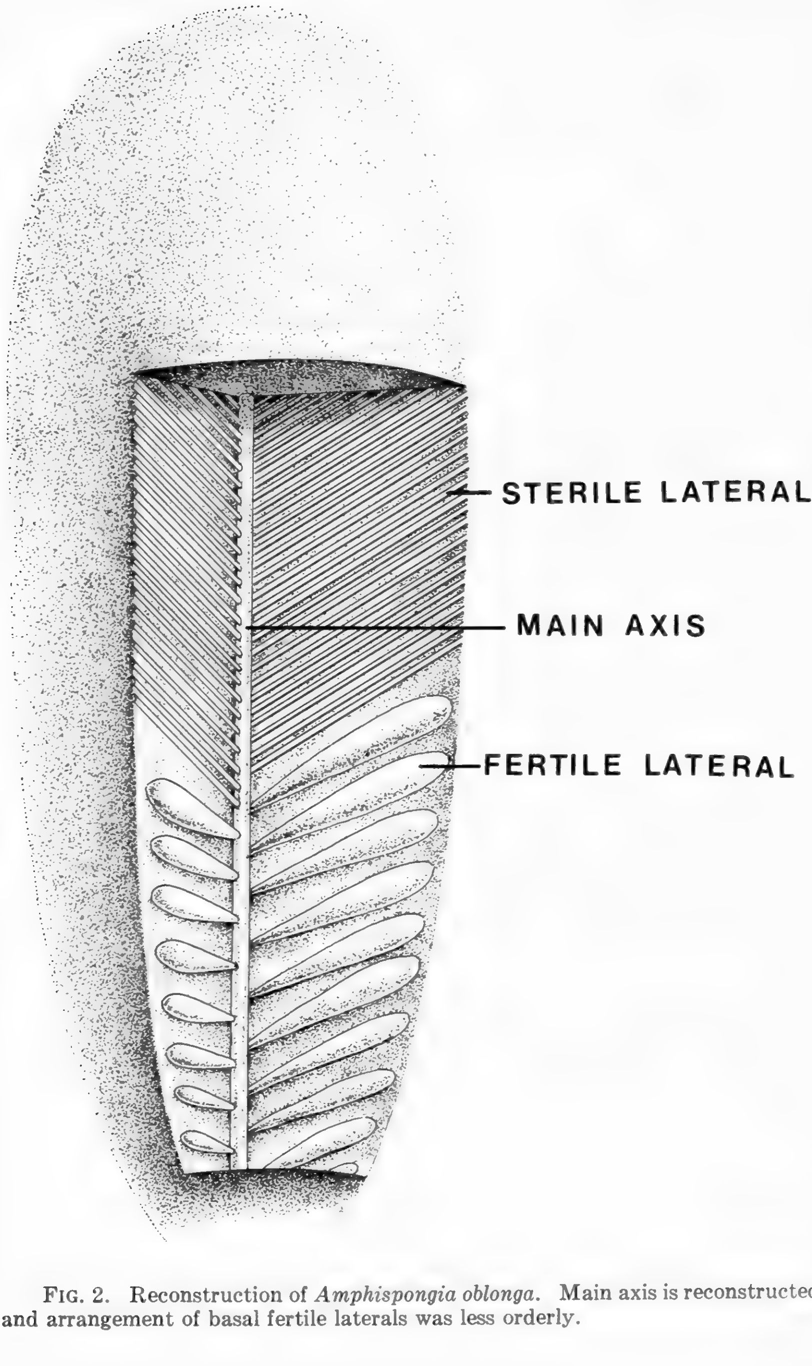

FIG. 2. Reconstruction of *Amphispongia oblonga*. Main axis is reconstructed, and arrangement of basal fertile laterals was less orderly.

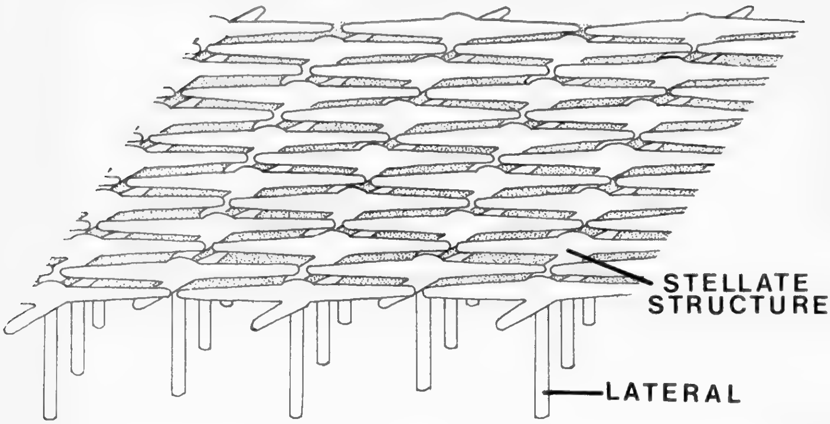

FIG. 3. Reconstruction of the termini of the upper filamentous sterile laterals of *Amphispongia* showing the stellate structures.

of mostly four ribs predominantly on upper laterals; Silurian, Ludlow, Scotland; one species.

Amphispongia oblonga Salter, 1861. Figures 1–3.

Amphispongia oblonga Salter, 1861, Mem. Geol. Surv. Great Brit. Scotland, pp. 133, 135–136, pl. 2, figs. 3, 3a–b; Bigsby, 1868, Thesaurus Siluricus, p. 194; Murchison, 1872, Siluria, pp. 159, 509; Hinde, 1883, Cat. foss. sponges, pp. 154–156, pl. 33, figs. 12, 12a–d; Hinde, 1887, Mono. Brit. fossil sponges, part 1, pp. 16, 31, 47, pl. 3, figs. 3, 3a–f; Hinde, 1888, Mono. Brit. fossil sponges, part 2, pp. 131–132, 186; Etheridge, 1888, Foss. Brit. Isles, p. 2; Nicholson and Lydekker, 1889, Man. Palaeontol., **1**, p. 177, figs. 63c–d; Rauff, 1894, Palaeosp., pp. 276–278, text-figs. 56–57, pl. 7, figs. 1–4; Ulrich, 1895, Geol. Minn., **3**, pt. 1, p. 74; Lamont, 1947, Geol. Mag., **84**, no. 4, p. 194; Laubenfels, 1955, Treat. Inv. Paleo., part E, p. 77, text figs. 59,3a–c; Lamont, 1961, Lex. stratigr. intern., p. 71; Mitchell, 1962, Mem. Geol. Surv. Scotland, p. 138; Anonymous, 1966, Brit. Palaeoz. fossils, p. 41, pl. 15, fig. 8.

Amphispongia sp. indet. Bigsby, 1868, Thesaurus Siluricus, p. 3.

Definition.—Same as genus.

Description.—THALLUS: All specimens are ovate or claviform and are now compressed (fig. 1). The thalli in life were considerably thinner than their present preserved state. The length of the thallus varies from 10 mm. (Nitecki, this paper) to 60 mm. (Hinde, 1883; Rauff, 1894). Because the fossils are highly flattened, the measurements of the widths are less meaningful and vary from 5 mm. (Nitecki) to 23 mm. (Hinde, 1883; Rauff, 1894). No attachment rhizoid is preserved.

MAIN AXIS: The main axis is not preserved; it is assumed to have been thin in a manner shown in Figure 2. However, it could have been apically robust.

LATERALS: Two distinct sets of laterals are present. The lower set consists of very regular, claviform, and relatively large branches. These expand gently toward the outside, and their pointed ends are clustered, apparently at random around the central axis (fig. 1). They vary in length from 1.5 to 5.0 mm. and in width from 0.5 to 1.0 mm.

The upper set of laterals consists of very thin, filamentous branches. The bases of stellate structures and the individual ribs form (on thalli of better preserved specimens) a distinct set of horizontal, sometimes vertical lines (fig. 3). These indicate that the upper laterals are borne in whorls.

STELLATE STRUCTURES: Stellate structures are present on upper and lower laterals. However, they are frequently detached from the lower branches, and hence are seldom preserved in that area of the thallus. Stellate structures in the upper part of the body consist predominantly of four ribs arranged in a cross (fig. 3). Often there are only three ribs present, but never less than two. The ribs are arranged almost in a plane, but one set is always above the other. The horizontal ribs are exterior, the vertical ribs are interior in position. Generally the ribs are close together but sometimes the ribs are apart. The horizontal outer lines formed by the ribs are more common than the vertical lines. The ribs vary in length from 0.25 mm. to 1.0 mm. and are on the average 0.1 mm. thick. The horizontal ribs are almost always longer.

GAMETANGIA: Gametangia are not observed in any specimens. It is assumed that they were borne in lower robust, calcified laterals, which are considered gametangial rays. The upper, thin branches are considered young sterile laterals.

CALCIFICATION: The calcification is heaviest on lower laterals. Upper laterals appear uncalcified, or only very weakly calcified. The stellate structures of the upper laterals are, however, well calcified.

Preservation: All specimens are preserved as casts. Associated calcareous invertebrates such as brachiopods, clams, and snails are also preserved only as casts. All *Amphispongia* are of fairly uniform size, and no small specimens are observed. It cannot be determined whether this is due to a sorting process or to the lack of calcification in the younger individuals.

Stratigraphic position and locality.—North Esk Inlier; North of North Esk and Weatherlaw Linn Junction; and Deer Hope Burn; all Pentland Hills, near Edinburgh, Scotland.

Silurian; Upper Llandovery Series, Deerhope siltstones (Lamont, 1961).

Material.—Numerous individuals on rock specimens; rock specimens nos. 1897.32.775 to 1897.32.790 in the Royal Scottish Museum, Edinburgh, Scotland.

Matrix.—Massive silty mudstone, with apparently little or no bedding.

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Dr. Charles D. Waterston of the Royal Scottish Museum generously loaned the specimens used in this study. Dr. Robert M. Finks of the American Museum of Natural History read the manuscript critically. Mr. Richard Roesener, Field Museum, drew Figures 2 and 3.

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